Evidence for the Evolution of Bdelloid Rotifers Without Sexual Reproduction or Genetic Exchange

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The Class Bdelloidea of the Phylum Rotifera is the largest metazoan taxon in which males, hermaphrodites, and meiosis are unknown. We conducted a molecular genetic test of this indication that bdelloid rotifers may have evolved without sexual reproduction or genetic exchange. The test is based on the expectation that after millions of years without these processes, genomes will no longer contain pairs of closely similar haplotypes and instead will contain highly divergent descendants of formerly allelic nucleotide sequences. We find that genomes of individual bdelloid rotifers, representing four different species, appear to lack pairs of closely similar sequences and contain representatives of two ancient lineages that began to diverge before the bdelloid radiation many millions of years ago when sexual reproduction and genetic exchange may have ceased.

Few species of animals or plants reproduce only asexually—and those that do seldom make up an entire genus, let alone a taxon of higher rank (*1*–*3*). These observations have been taken to mean that the loss of sexual reproduction is a dead end in evolution, leading to early extinction. Against this generalization, the entire Class Bdelloidea of the Phylum Rotifera stands out as an apparently radical exception (*4*), an "evolutionary scandal" (*5*).

The Rotifera, a protostome phylum, includes four monophyletic groups: Class Bdelloidea, Class Monogononta, Class Seisonida, and the Acanthocephala (*6*–*10*). Seisonids and acanthocephalans reproduce sexually and monogononts reproduce both sexually and asexually, but only asexual reproduction is known in bdelloids (*11*).

The Class Bdelloidea, comprising four families, 18 genera, and some 360 described species (*12*–*14*), is by far the largest metazoan taxon in which no evidence of sexual reproduction has been found (*2*, *15*, *16*). Eggs are produced from oocytes in well-differentiated ovaries by two mitotic divisions with no chromosome synapsis and no reduction in chromosome number, each oocyte giving rise to one egg and two polar bodies (*17*, *18*). Bdelloid rotifers have existed for at least 35 to 40 million years, the age of the oldest amber in which they have been identified (*19*).

Bdelloids are found in fresh water and moist terrestrial habitats worldwide and are easily recognized by their characteristic ciliated head structure. Individuals range from 0.1 to 1 mm in length and have about 1000 nuclei, with muscles, ganglia, tactile and photosensitive sensory organs, feeding and swimming structures, digestive and secretory organs, and gonads. The genomic DNA content in the species in which it has been measured is about 1000 megabase pairs (*20*, *21*). Figure 1 shows the four species used in this study, representing three of the four bdelloid families.

The failure to observe males, hermaphrodites, and meiosis throughout the class, although remarkable, does not exclude rare or unrecognized forms of sexual reproduction or some other mode of genetic exchange. Demonstration that bdelloid rotifers engage in sexual reproduction would put to rest the principal apparent exception to the prevailing view that genetic exchange is essential for evolutionary success. Conversely, demonstration that bdelloids evolved without sexual reproduction would challenge this central tenet of current evolutionary theory and would provide a system to test hypotheses for why sexual reproduction is so nearly universal and why other asexual species appear to suffer early extinction (*1*, *2*, *22*, *23*).

Here, we report a test of the possibility that bdelloid rotifers evolved without sexual reproduction or genetic exchange, based on the analysis of nucleotide sequences in individual genomes of diverse bdelloid species.

Experimental approach. In sexually reproducing species, recombination and segregation allow random genetic drift to drive selectively neutral alleles toward fixation or extinction, limiting the divergence between allelic sequences caused by recurring mutation (*24*). Reported species averages for synonymous site diversity (corresponding to average synonymous site heterozygosity if mating is random) in a wide variety of invertebrate and vertebrate species range from 0.1 to 4% (*25*–*29*).

In contrast, segregation can no longer occur in a lineage that has abandoned sexual reproduction and in which reproduction is only mitotic and is without nonsister exchange. After millions of years under these conditions, descendants of formerly allelic sequences within individual genomes, if not lost by deletion, gene conversion, or nondisjunction, will be highly divergent. Suppose, for example, that sex and genetic exchange were abandoned in a diploid ancestor of modern bdelloids 80 million years ago and that the average rate of neutral nucleotide substitution was 5×10^{-9} per site per year. In that case, individual genomes will no longer be made up of closely similar haplotypes. Instead, ignoring any contribution from preexisting heterozygosity and correcting for multiple substitutions at the same site, individual bdelloid genomes will contain descendants of formerly allelic sequences differing at about 50% of neutral sites (*29*).

Sequence divergence in genomes of bdelloid and nonbdelloid rotifers was investigated in four genes: *hsp82* (82-kD heat shock protein), *tbp* (TATA-box binding protein), *rpol3I* (RNA polymerase III large subunit), and *tpi* (triosephosphate isomerase). BLAST searches of all invertebrate sequences in available databases, including the complete genome sequences of *Caenorhabditis elegans and Drosophila melanogaster*, revealed no species in which any of these genes is accompanied by a paralog that arose since the origin of metazoans.

The experimental procedure was intended to isolate and sequence every copy of a given gene

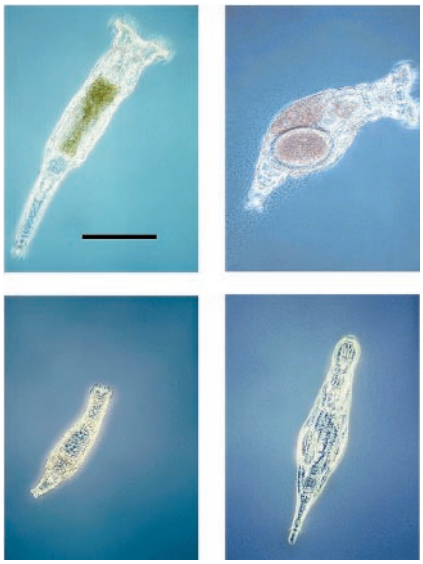

Fig. 1. Adult bdelloid rotifers of four species. Clockwise from upper left: *Philodina roseola* (Philodinidae) (eating algae), *Macrotrachela quadricornifera* (Philodinidae) (the large oval is a mature egg), *Adineta vaga* (Adinetidae), and *Habrotrocha constricta* (Habrotrochidae). Scale bar, 100 μm.

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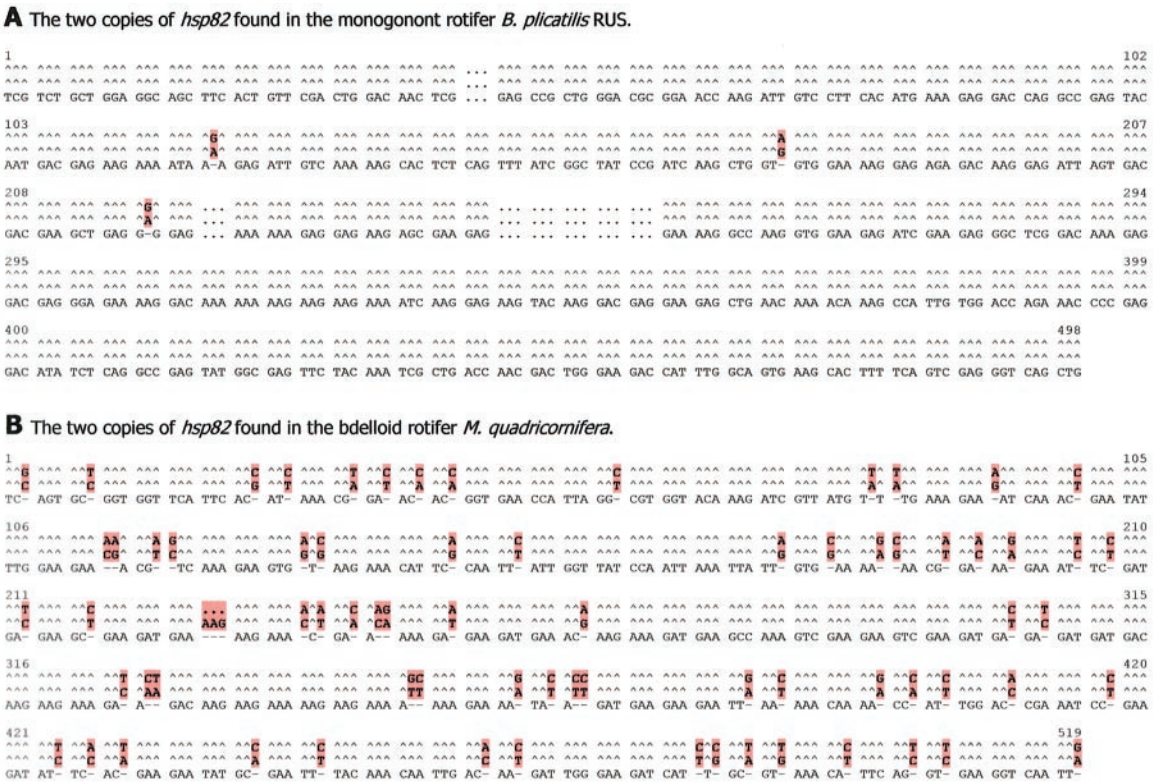

Fig. 2. Sequences of the two copies of *hsp82* found in (**A**) the monogonont rotifer *B. plicatilis* RUS and (**B**) the bdelloid rotifer *M. quadricornifera*. For each species, the copies are aligned codon by codon with the consensus beneath; identities are indicated as carets (^) and differences are shaded in red. Gaps are inserted in the *B. plicatilis* sequences to maintain register with the *M. quadricornifera* sequences.

present in the genome of a single individual of each species. DNA was extracted from a population recently propagated from a single individual or, in the case of some of the nonbdelloid species, prepared from a small natural isolate or a single animal. For each gene, 24 to 38 amplicons from two to four polymerase chain reaction (PCR) amplifications were cloned in plasmids and sequenced in both directions (*30*). As a measure of neutral difference in coding regions, we used the uncorrected percentage difference at fourfold degenerate sites, here designated D4, a quantity that is slower to saturate and less sensitive to transition-transversion bias than are differences at twofold and threefold degenerate sites (*31*). For the genes examined, 11 to 18% of all coding sites are fourfold degenerate.

Table 1. Divergence of *hsp82* copies in sexually reproducing rotifers. Percent difference (%) is indicated above the total number of differences found (no.) in each species at all nucleotide sites (Total), synonymous sites (Syn.), and fourfold degenerate sites (D4). Average sequence differences for the *D. pseudoobscura* region corresponding to *D. melanogaster* codon positions 1 to 270 (the longest length available) are calculated for 11 isolates reported in (*28*).

Species	Length examined (bp)	Difference (%/no.)		
		Total	Syn.	D4
B. plicatilis AUS	888	0.4 3	0.3 1	0.7 1
B. plicatilis RUS	498	0.3 3	0.6 1	2.0 1
B. calyciflorus	843	0.0 0	0.0 0	0.0 0
E. ehrenbergi	873	0.6 5	1.6 5	2.4 2
S. socialis	846	0.6 5	1.7 5	2.2 2
S. nebaliae	888	0.1 1	0.3 1	0.0 0
M. moniliformis	873	0.0 0	0.0 0	0.0 0
Average		0.3	0.7	1.0
D. pseudoobscura (SD)		0.2 (0.1)	0.5 (0.3)	0.5 (0.6)

Sequence divergence of *hsp82*. We examined *hsp82* in four bdelloid species representing the three major families within the class and, for comparison, seven species of sexually reproducing rotifers (*30*). The region examined was the 843- to 888-bp segment corresponding to *D. melanogaster* codons 13 to 302, except in *Macrotrachela quadricornifera* and *Brachionus plicatilis* RUS, for which the regions examined were the 518- and 498-bp segments, respectively, corresponding to *D. melanogaster* codons 152 to 320.

Genomes of each of the seven sexually reproducing rotifers were found to contain either two nearly identical *hsp82* sequences, as depicted for *B. plicatilis* RUS in Fig. 2A, or only a single sequence (Table 1). The highest D4 in this group of nonbdelloid rotifer genomes was 2.4% (average 1%). A similar average D4 (0.5%) may be calculated for the corresponding region of *hsp82* in a natural population of *Drosophila pseudoobscura* (*28*).

Findings for bdelloid rotifers were very different. Each of the four bdelloid genomes examined contains two or more highly divergent copies of *hsp82*. No copies were found that are as closely similar to each other as those in nonbdelloid rotifers (Tables 1 and 2). Two copies were found in *M. quadricornifera*, differing at fourfold degenerate sites by 54% (Fig. 2B). Three copies were found in *Adineta vaga* and *Habrotrocha constricta* and four in *Philodina roseola*. The highest values of D4 between *hsp82* copies in each of these three bdelloid genomes are 30, 26, and 49%, respectively, and the corresponding lowest values are 6.0, 6.6, and 3.5%. All three copies of *hsp82* in *A. vaga* contain a 57- to 58-bp intron, and the divergence between intron copies parallels D4 for adjacent exons.

In agreement with the above results, Southern blots of genomic DNA probed with *hsp82* revealed restriction fragments diagnostic for each of the four copies of *hsp82* in *P. roseola* and for each of the three copies in *H. constricta* and no other fragments (*32*). As expected, Southern blots of the monogonont *B. plicatilis* AUS showed only a single fragment, corresponding to the two nearly identical copies of *hsp82* in this species.

Relative rate tests show no significant difference between bdelloids and monogononts in *hsp82* fourfold degenerate substitution rates, using the acanthocephalan *M. moniliformis* as an outgroup (*32*). There is therefore no indication that nucleotide mutation rates in bdelloids differ from those in monogononts.

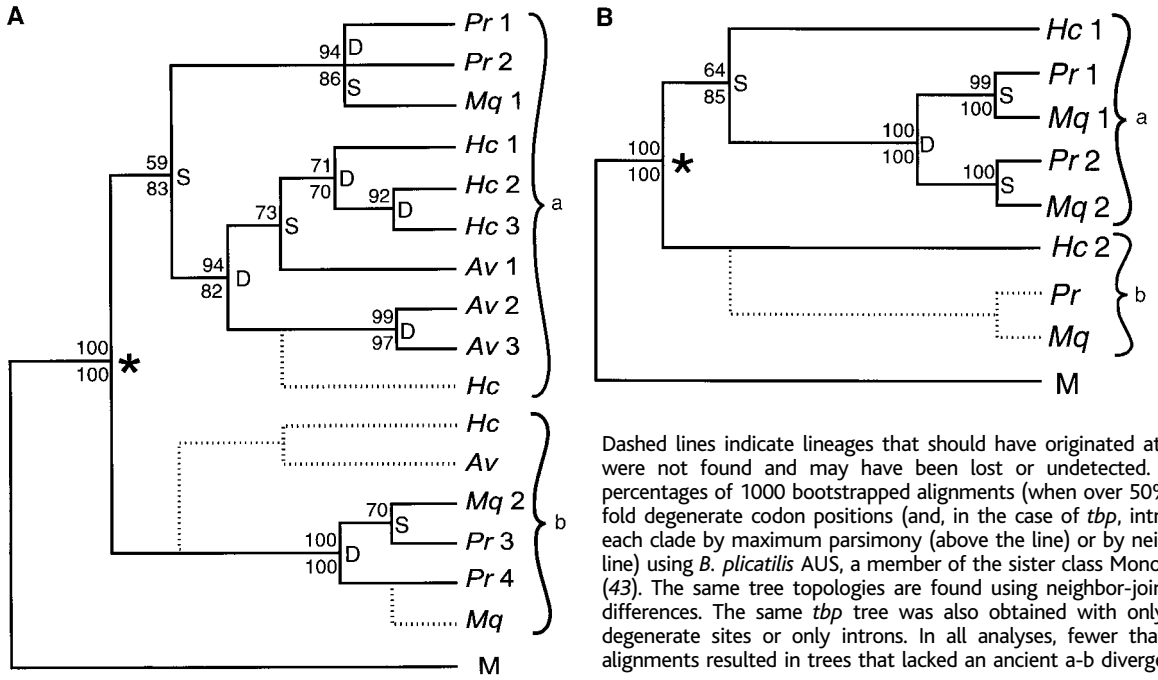

Fig. 3. Phylogeny of *hsp82* and *tbp* in bdelloid rotifers. (**A**) *hsp82*. (**B**) *tbp*. The ancient lineages a and b of *hsp82* and of *tbp* began to diverge at the nodes indicated (*). Both lineages of *hsp82* are still present in genomes of *P. roseola* and *M. quadricornifera*, as are both lineages of *tbp* in *H. constricta*. Other nodes are attributed to duplication events (D) or to separations of taxa (S). Dashed lines indicate lineages that should have originated at species separations but were not found and may have been lost or undetected. Numbers at nodes are percentages of 1000 bootstrapped alignments (when over 50%) of fourfold and threefold degenerate codon positions (and, in the case of *tbp*, intron positions) supporting each clade by maximum parsimony (above the line) or by neighbor-joining (below the line) using *B. plicatilis* AUS, a member of the sister class Monogononta, as an outgroup (*43*). The same tree topologies are found using neighbor-joining of synonymous site differences. The same *tbp* tree was also obtained with only fourfold and threefold degenerate sites or only introns. In all analyses, fewer than 10% of bootstrapped alignments resulted in trees that lacked an ancient a-b divergence.

Sequence divergence of *tbp*, *rpol3I*, and *tpi*. Two divergent copies and no closely similar copies of each of these three genes were found in individual bdelloid genomes. The region of *tbp* corresponding to *D. melanogaster* codons 187 to 295 was examined in the bdelloids *P. roseola*, *M. quadricornifera*, and *H. constricta* and in the monogonont *B. plicatilis* AUS. D4 values for *tbp* in the bdelloid genomes are 14, 16, and 44%, respectively. Each copy contains two introns of about 60 bp, and the average difference between intron copies is about equal to D4 for the surrounding exons (Table 3). Only a single *tbp* sequence, without introns, was found in *B. plicatilis*.

The *tpi* and *rpol3I* genes were examined only in the bdelloid *P. roseola*, giving D4 values of 73 and 12%, respectively. Both copies of *tpi* have three introns of about 60 bp, and the average difference between intron copies is 36% (Table 4).

Nucleotide differences between gene copies in coding regions of all four genes examined in bdelloid genomes are mainly at codon third positions and are distributed throughout the sequenced regions, as illustrated in Fig. 2B. No in-frame stop codons are present in any copy, synonymous substitutions consistently outnumber replacement substitutions, and amino acid sequences closely match those of the corresponding genes in other organisms. Evidently, all copies are functional. It may be that nonfunctional copies are deleterious even in the presence of functional copies and are eliminated by selection, consistent with the partial dominance of deleterious recessives observed in heterozygotes of diverse species (*33*–*35*). Also, in the absence of segregation, strong heterotic interactions may evolve (*1*), making the inactivation of gene copies involved in such interactions disadvantageous.

Phylogeny of *hsp82* and *tbp* in bdelloid rotifers. Relationships among the 12 copies of *hsp82* and among the 6 copies of *tbp* sequenced in bdelloid rotifers are depicted in Fig. 3. All copies of *hsp82* belong to one or the other of two ancient lineages, designated a and b, that began to diverge after the separation of bdelloids and monogononts but before the separation of the bdelloid families we examined (Fig. 3A). Representatives of both lineages are present in individual genomes of *P. roseola* and *M. quadricornifera*. In addition, apparent duplications and losses of *hsp82* occurred occasionally during the bdelloid radiation.

As with *hsp82*, the six copies of *tbp* identified in bdelloids belong to one or the other of two ancient lineages, also designated a and b, that began to diverge after the separation of bdelloids and monogononts but before the bdelloid radiation (Fig. 3B). Descendants of both *tbp* lineages are present in the genome of *H. constricta*.

The average fourfold degenerate difference between the a and b lineages of *tbp* (53%, SD 5.5) is not significantly different from that between the a and b lineages of *hsp82* (49%, SD 4.2), consistent with the indication from phylogenetic analysis that the a and b lineages of both genes began to diverge during the same interval. For com-

Table 2. Divergence (D4) of *hsp82* copies in bdelloid rotifers. Each copy is designated by the first letters of the genus and species followed by a number. Divergences between copies within the same genome are shown in boldface. The *A. vaga* intron is located after *D. melanogaster* codon position 88; the total divergence between copies Av1 and Av2, Av1 and Av3, and Av2 and Av3 in the intron is 47, 49, and 5.3%, respectively. A 58-bp intron is present after *D. melanogaster* codon position 241 in Hc1. Neither intron is present in any other rotifer examined, indicating that they appeared late in bdelloid evolution. No *hsp82* introns were found in any nonbdelloid rotifer.

	Coding sequence											
Length (bp)	Mq1 516	Mq2 519	Pr1 873	Pr2 873	Pr3 879	Pr4 879	Hc1 873	Hc2 873	Hc3 873	Av1 870	Av2 870	Av3 870
Mq1		**54**	4.9	3.7	53	51	54	56	60	57	57	63
Mq2			51	58	0	7.1	55	49	47	47	47	51
Pr1				**3.5**	**46**	**44**	46	41	44	45	42	46
Pr2					**49**	**47**	48	42	45	46	43	46
Pr3						**6.0**	54	47	47	52	48	49
Pr4							53	46	46	50	47	48
Hc1								**23**	**26**	29	32	34
Hc2									**6.6**	31	28	30
Hc3										32	26	28
Av1											**29**	**30**
Av2												**6.0**

Table 3. Divergence of *tbp* copies in bdelloid rotifers. Divergences between copies within the same genome are shown in boldface. Values are D4 except for introns, for which total difference is given. Intron 1 is located after *D. melanogaster* codon position 271 and intron 2 after the second nucleotide of codon 295, a conserved intron-exon boundary (*39*).

	Coding sequence						Intron 1						Intron 2					
Length (bp)	Pr1 327	Pr2 327	Mq1 327	Mq2 327	Hc1 327	Hc2 327	Pr1 70	Pr2 70	Mq1 70	Mq2 70	Hc1 53	Hc2 60	Pr1 63	Pr2 67	Mq1 63	Mq2 67	Hc1 46	Hc2 46
Pr1		**14**	6.0	14	51	56		**7.1**	5.7	11	33	57		**11**	3.2	7.9	61	70
Pr2			16	0	39	54			13	4.3	31	55			9.5	3.0	57	67
Mq1				**16**	50	58				**17**	37	60				**9.5**	61	67
Mq2					39	55					33	55					57	67
Hc1						**44**						**47**						**54**

parison, the average D4 values between bdelloids and the monogonont *B. plicatilis* AUS for *hsp82* and *tbp* are 75% (SD 6) and 79% (SD 3), respectively.

Discussion. We find that genomes of rotifers of the Class Bdelloidea are strikingly different from genomes of rotifers belonging to the other three classes of the phylum, in which reproduction is known to be obligately or facultatively sexual, and from genomes of sexually reproducing species generally.

First, nearly identical pairs of genes were found in nonbdelloid rotifers, as expected in sexually reproducing diploids, but were not found in bdelloids. Even the most similar copies found in any bdelloid genome are more divergent than the most divergent pair found in any other rotifer (Tables 1 to 4). Although not conclusive, a further suggestion that bdelloid genomes are not composed of allelic pairs of haplotypes comes from the observation that at least 3 of the 13 chromosomes in the karyotype of *P. roseola* and 2 of the 13 chromosomes in the karyotype of *Habrotrocha rosa* have no morphological homologs (*18*, *36*).

A formal possibility that could account for a lack of allele pairs in individual genomes is that bdelloids are haploid females of sexually reproducing species that have an evanescent or unrecognized diploid form. The failure to observe male bdelloids and the lack of haploid females in any metazoan life cycle make this possibility remote.

A second remarkable feature of bdelloid genomes is the consistent presence in individual genomes of divergent copies of each of the four genes examined, a condition not encountered in any of the nonbdelloid rotifers (Tables 1 to 4) or in reported sequences of any other invertebrate. Although several all-female lines in diverse animal taxa are known to have arisen as alloploids (*1*, *2*), the consistent finding of highly divergent gene copies in bdelloids cannot be attributed to recent species hybridization, for this would require a multitude of separate hybridizations between highly divergent parents and the disappearance of or failure to recognize the parental sexual species. Moreover, phylogenetic analysis of *hsp82* and *tbp*, the two genes examined in more than one bdelloid species, reveals that each copy of *hsp82* and each copy of *tbp* belongs to one or the other of two lineages that began to diverge before the bdelloid radiation and after the separation of bdelloids from monogononts (Fig. 3). These ancient divergences cannot be attributed to speciation because both *hsp82* lineages are still present in individual genomes of *P. roseola* and *M. quadricornifera* and both *tbp* lineages are still present in *H. constricta*. Such stable association could result, however, if the two lineages descend from ancient duplications or from an ancient polyploid ancestor or if they descend from former allele pairs that neither recombined nor segregated throughout bdelloid evolution. In addition, apparent duplications and losses have occurred occasionally during the bdelloid radiation as may have resulted, for example, from nondisjunction.

Our results exclude the possibility that bdelloid rotifers are ordinary diploids that engage in rare or cryptic sex. It remains possible that, unlike any other metazoan that has been examined, bdelloids are ancient polyploids or diploids with ancient duplications of every gene we studied and that they engage in some elusive form of sexual reproduction but are unusually homozygous. However, consistent with the failure to find males, hermaphrodites, or meiosis, it appears more plausible to interpret our findings as further evidence that the Class Bdelloidea has evolved for tens of millions of years without sexual reproduction or genetic exchange between former alleles.

Table 4. Divergence of *rpol3I* and *tpi* copies in *P. roseola*. Introns are located in both copies of *tpi* at three conserved positions, numbered after (*40*). Copy 1 of *tpi* contains two additional introns, 61 and 59 bp in length, at conserved positions 3 and 9, respectively. No introns were found in *rpol3I*. For both *tpi* and *hsp82*, the differences in the number of introns between gene copies in individual bdelloid genomes are comparable to those between species with similarly high levels of synonymous sequence difference in surrounding exons (*41*, *42*).

	Length examined (bp)		D4 or Diff. (%)
	Copy 1	Copy 2	
rpol3I	654	654	12
tpi coding	510	510	73
tpi intron 4	64	69	42
tpi intron 6	53	69	37
tpi intron 10	54	55	29

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30. The rotifers examined were as follows. Bdelloidea: *Philodina roseola*, *Macrotrachela quadricornifera*

(Philodinida, Philodinidae), *Habrotrocha constricta* (Philodinida, Habrotrochidae), and *Adineta vaga* (Adinetida, Adinetidae). Monogononta: *Brachionus plicatilis* strains AUS and RUS, *Brachionus calyciflorus* (Ploima, Brachionidae), *Eosphora ehrenbergi* (Ploima, Notommatidae), and *Sinantherina socialis* (Flosculariacea, Floscullariidae). Seisonida: *Seison nebaliae*. Acanthocephala: *Moniliformis moniliformis*. Attribution and provenance are available at *Science* Online at www.sciencemag.org/feature/data/1050064.shl. Bdelloids, *B. calyciflorus*, and both strains of *B. plicatilis* were kept in large (10^4 to 10^5) cultures grown from single eggs or single individuals after 10 serial passages through sterile water in microtitre wells. Culture conditions and DNA extraction procedures are described elsewhere (*21*, *36*). DNA was extracted from a single colony of *S. socialis* and from single field collections of *E. ehrenbergi* and *S. nebaliae* (*10*). Primer sequences and PCR protocols are available from the authors or at *Science* Online at www.sciencemag.org/feature/data/1050064.shl. Each sequence found was represented in at least five cloned amplicons from at least two amplifications, except *hsp82* copy 2 of *P. roseola*, which was found only in the cosmid library. Occasionally, a single PCR clone differed from a set of otherwise identical clones at one or two sites, which could be attributed to an error rate of about 0.0003 per nucleotide, similar to the error rate reported in other PCR cloning experiments (*37*, *38*). The *hsp82* region in 36 phage lambda clones and 25 cosmid clones selected from genomic libraries of *P. roseola* was also sequenced.

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43. DNA sequences were aligned (*10*) and analyzed with the Wisconsin Package 10.0 (Genetics Computer Group) and the PHYLIP v3.57 package of J. Felsenstein. Uncorrected difference at fourfold degenerate sites (D4) was determined from pair-wise comparisons with DIVERGE. Phylogenetic analyses used all codon third positions belonging to conserved fourfold or threefold degenerate codon classes plus third positions in those few cases where a codon in a single bdelloid sequence differed from a fourfold or threefold degenerate class by no more than a single substitution. Distances for neighbor-joining were adjusted for multiple mutations with the Kimura two-parameter model with rates following a gamma distribution with a coefficient of variance (CV) of 1.41 estimated for both genes from the maximum likelihood algorithm in PAUP*. The same tree topologies, with similar bootstrap support, are found with a range of CV.

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Rocks from the Mantle Transition Zone: Majorite-Bearing Xenoliths from Malaita, Southwest Pacific

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Rocks containing high-pressure mineral assemblages derived from the mantle transition zone between depths of about 400 and 670 kilometers occur as xenoliths and megacrysts on the island of Malaita in the southwest Pacific on the Ontong Java Plateau. Observed ultrahigh pressure mineral chemistries include majorite, calcium- and magnesium-perovskite, aluminous silicate phases, and microdiamond. Based on an empirical barometer, majoritic garnets in these xenoliths record pressures of up to 22 gigapascal. The occurrence of material with perovskite chemistry and several enigmatic aluminous phases indicates pressures of up to 27 gigapascal. Samples were brought to the surface at about 34 million years ago by potassic ultramafic magmas, which evidently originated in the lower mantle.

Xenoliths, the main direct source of information about mantle mineralogy, are predominantly derived from the top of the upper mantle, from depths of ~150 to 200 km (*1*, *2*), although some have been reported from depths of ~400 km (*3, 4*). Mineral inclusions in diamond are generally interpreted to yield a record of phase relations at depths of 150 to 200 km, equivalent to pressures of ~5.5 to 7 GPa (*5, 6*). Extremely rare single-mineral inclusions of ferropericlase, Mg-Si perovskite, Ca-Si perovskite, and magnesiowustite have recently been discovered in diamond derived from the lower mantle (*7*). Most deep xenoliths and diamonds are transported in kimberlites and lamproites that intrude continental lithosphere (*1, 8*). Here, we describe an extensive suite of garnetite and rare garnet peridotite xenoliths that contain majoritic and other ultrahigh pressure mantle assemblages, indicating that these rocks sample the mantle transition zone in an oceanic environment.

Geology and Locality

The xenoliths and macrocrysts occur in ~34 Ma (million years ago) alnöite pipes and sills (*9*), which cut Cretaceous Ontong Java Plateau basalts, Miocene limestones, and mudstones on the island of Malaita, southwest Pacific (Fig. 1). The oceanic Ontong Java Plateau covers an area of 1.28×10^6 km^2 to the northeast of the Solomon Island archipelago and Bougainville Island (Fig. 1) and is one of the largest plume-generated intraplate igneous provinces preserved on the planet. Volcanic activity on the Ontong Java Plateau commenced at ~122 Ma, and a second major pulse of magmatism occurred at 90 Ma (*10*). At this time, the Ontong Java Plateau was located several thousand km farther east in the central Pacific Ocean (*11*). Igneous rocks on Malaita have a plume origin, distinct from the arc-generated islands in the Solomon Archipelago (*10*).

Seismic reflection profiles show that Ontong Java Plateau basalts are cut by numerous distinctive plug-like bodies that vary in diameter up to ~2.5 km (*11*) and may be kimberlite pipes (*12*). Alnöitic magmatism at ~34 Ma occurred before collision of Malaita with the Indo-Australian plate ~10 Ma (*13*), and before initiation of geologically unrelated Solomon Islands arc magmatism (*12, 14*).

We obtained mantle xenoliths and garnet macrocrysts from stream gravels in several drainage systems from the north central and eastern parts of the island (*15*), where a number of pipes have been mapped. The studied ultramafic xenoliths are ovoid in shape and range in diameter from <1 to 30 cm. Compositions include spinel lherzolite, pyroxenite intergrowths, spinel bearing eclogite, and rare garnet lherzolite. The macrocrysts suite includes pyrope, subcalcic diopside, augite, orthopyroxene (bronzite), ilmenite, clinopyoxene-ilmenite intergrowths, phlogopite, olivine, and zircon (*14, 16, 17*). Many of the macrocrysts exhibit a distinctive surficial polish that is interpreted to have been caused by abrasion during turbulent magmatic emplacement. Garnet macrocrysts are typically elongate and range in size from ~1 cm by 0.5 cm by 0.5 cm to larger than 20 cm by 10 cm by 10 cm. Except for olivine, all of the other macrocrystal phases are extremely fresh.

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